

NOTES ON THE BIOLOGY OF SOME
SEAGRASS-DWELLING CRUSTACEANS
(STOMATOPODA AND DECAPODA)
FROM CARIBBEAN PANAMA

Loren D. Coen and Kenneth L. Heck, Jr.

Abstract.—A year-long sampling program in seagrass meadows along the Caribbean coast of Panama yielded two stomatopod and 58 decapod species in 45 genera and 22 families, a number of which was previously unreported from Panamanian waters. Though not complete, this annotated list provides information on size, seasonality, reproductive state, and presence of parasites. High species affinities with recent collections from Bermuda and the Carolinas exist. Specifically, 59% of the species treated here are reported from the Carolinas and 64% from Bermuda; however, no regional endemics were found. Range extensions are made for several species. Recent literature and taxonomy are reviewed for most species discussed.

Abele, in a symposium volume on the Panamic biota in 1972, pointed out that almost no information was available at that time on the crustaceans of Panama. In recent years there have been publications on the brachyuran fauna of the Bahamas (Garth 1978) and the north coast of Colombia (Lemaitre 1981), and on the decapod fauna of Bermuda (Markham and McDermott 1981). Yet, with the exception of Gore and Abele's (1976) publication on the porcellanid crabs of Panama, and Gore's (1982) recent study on the Porcellanidae of Central America, our knowledge of the Panamanian crustacean fauna, especially on the Caribbean coast, remains nearly as limited as when Abele made his comments ten years ago.

Here we provide new information on a number of poorly known decapod and stomatopod crustaceans found primarily in seagrass habitats along the Caribbean coast of Panama. Included are data on size, reproductive condition, habitat, and other observations on the natural history of the 60 species treated here. This is clearly a small percentage of the total decapod and stomatopod fauna of the Caribbean coast of Panama and our list is in no way comprehensive. However, we believe that it does provide an indication of the species commonly found in subtidal seagrass habitats along the Caribbean Panamanian coast. Other information on the species treated here has been previously published by Heck (1977, 1979) and Heck and Wetstone (1977).

Study Sites

Sites consisted of vegetated subtidal meadows within 30 m of the shore. Study areas were located 20 km to the northeast of the Caribbean end of the Panama Canal (Fig. 1). Detailed descriptions of our stations 1-4 are provided by Heck (1977) and Weinstein and Heck (1979). Station 1 was seaward of a thick mangrove shoreline (*Rhizophora mangle* (L.)) and contained thick growths of *Thalassia*



Fig. 1. Location of collection sites along the Caribbean coast of Panama.

testudinum (König) and *Halimeda opuntia* (L.) with lesser amounts of *Syringodium filiforme* (Kützinger), *Udotea flabellum* (F.) (Ellis and Solander) and *Penicillus capitatus* (Lamarck). Sediments were mostly fine muds, and the site was protected from wave shock by a small patch reef. Station 2 was exposed to the most severe wave shock of our 5 study areas. Dominant vegetation included *T. testudinum* and *S. filiforme*. Sediments were calcareous sand with some larger coral and *Halimeda* fragments. Station 3 received the least wave shock among our 5 sites. *Thalassia testudinum* was the dominant plant, although *H. opuntia* and *H. incrassata* (Ellis) were also present. Sediments were coarse with many coral and *Halimeda* fragments. Station 4 was surrounded by reefs and located in the lee of two small islands. *Thalassia testudinum* was the dominant plant although *S. filiforme* was also present. Sediments were coarse with many coral fragments. Station 5 was located in a small cove lined with red mangroves (*R. mangle*). Vegetation was sparse, with some *T. testudinum* and *S. filiforme* present.

Salinities ranged from nearly 0‰ during heavy rains to nearly 38‰ during the dry season, although values were most often similar to open sea salinities (~38‰). Water temperatures ranged from about 27–31°C (see Glynn 1972, for additional information on the physical regime). Although the stations were subtidal, water depth rarely exceeded 2 m or became shallower than 1 m during any one tidal cycle.

Methods

Samples were collected by a 4.87 m otter trawl, with 19 mm stretch mesh wings and a 6.3 mm liner. Monthly samples (station 1–4) were taken during the period of July 1974–May 1975, according to the schedule described by Heck (1977). Station 5 was only sampled during July, August, and September. Samples were

taken diurnally, except for one set of night samples in May 1975 at stations 1, 2 and 3 (an average of 4 trawls per station). All samples were preserved in 10% formalin and later transferred to 70% isopropanol before identifications were made. All available specimens were identified, sex determined and measured to gather information on size at sexual maturity. By our criteria male shrimps were mature if the appendix masculina on the second pleopod was apparent (with a few exceptions, e.g., *Synalpheus* in which the appendix masculina is absent). Female shrimps were only separated into ovigerous and non-ovigerous categories. Maturity of anomuran and brachyuran crabs follows Abele and Blum's (1977) criteria. Male crabs were considered mature with the development of gonopods; females if the abdomen was covered by the sternum.

Most measurements are given for carapace length (cl), measured by dial caliper to the nearest 0.1 mm from posterior margin of the carapace to the postorbital margin. For crabs, carapace width (cw) includes the greatest width measured including spines. For hermit crabs, shield length (sl) was measured as in Provenzano (1959). Descriptions were not considered necessary but recent faunal summaries and classic monographs where these may be found are summarized (Table 1) as an aid to future works in the zoogeographical areas. The classification and nomenclature scheme used here has been adopted from *The Biology of Crustacea* (1982; L. G. Abele, pers. comm.) and Abele and Felgenhauer (1982).

Part of the collection was lost or badly damaged in transport from Panama, and resulting deficiencies are noted where appropriate in the text. Thus, many of the preliminary identifications (Heck 1977) done by authorities in the field are retained, though the specimens could not be measured or sexed.

ANNOTATED SPECIES LIST

SUPERORDER HOPLOCARIDEA

ORDER STOMATOPODA

Family Gonodactylidae

Gonodactylus lacunatus Mannins, 1966

Material.—Station 5; Sept; 1 male.

Measurements.—cl 5.4 mm.

Distribution.—From the western Atlantic, the Caribbean Sea, Yucatan, Nicaragua and Colombia; sublittoral to 50 m, though usually in shallower waters.

Family Pseudosquillidae

Pseudosquilla ciliata (Fabricius, 1787)

Material.—Stations 1, 3 and 4; Aug, Sept, Oct, Feb and Apr; 7 individuals.

Measurements.—Males, 4.3 to 7.9 mm cl; females, 5.0 to 7.3; juveniles, 3.4 to 3.5.

Habitat.—Shelly-sand, coralline algae, coral, though most often seagrasses.

Distribution.—From tropical oceans in the Indo-West Pacific, the western Atlantic, Bermuda, the Bahamas, Florida and western Africa; to 110 m, though primarily in shallower waters.

Table 1.—Brief summary of the carcinological literature (Decapoda) relating to the faunal area.*

Author(s)	# of species treated†	Taxonomic group discussed	Comments‡
FAUNAL SUMMARIES			
Abele 1970	154	Decapoda of northwestern Gulf of Mexico	a, k
Abele 1972a,b	485	Pacific and Caribbean Decapods of Panama	a
Felder 1973	143	Crabs and lobsters of the northwest Gulf of Mexico	a, k
Garth 1978	53	Brachyura of the Bahamas	a
Heck 1977	65	Decapoda, Caribbean Panama	f
Lamaitre 1981	96	Shallow-water Brachyura of Colombia	a
Markham and McDermott 1981	276	Decapoda of Bermuda	f
Park 1969	15	Portunidae of Biscayne Bay	a
Powers 1977	352	Crabs of the Gulf of Mexico	a
Rouse 1970	103	Littoral Crustacea of southwest Florida	a, k
Wass 1955	113	Decapoda of northwest Florida	a, k
Williams 1965	220	Decapoda of the Carolinas	a, k
TAXONOMIC WORKS (including monographs)			
Camp 1973	28	Stomatopoda of Florida (Hourglass Cruises)	a, k
Chace 1972	218	Shrimps of the Smithsonian-Bredin Expedition (Caribbean and West Indies)	a, k
Coutière 1909	45	American <i>Synalpheus</i> species	a, k
Gore and Abele 1976	43	Pacific Panama and adjacent Caribbean, Procellanidae	a, k
Gore and Scotto 1979	22	Western Atlantic Parthenopidae	a, k
Haig 1960	85	Eastern Pacific Porcellanidae	a, k
Holthuis 1958	5	Calappidae of the West Indies	a, k
Holthuis 1959	121	Decapoda of Suriname (Dutch Guiana)	a, k
Lemaitre <i>et al.</i> 1982	12	Provenzano group of pagurid crabs	a, k
Lyons 1970	6	Scyllaridae of Florida (Hourglass Cruises)	a, k
Manning 1961	2	Genus <i>Leander</i>	a, k
Manning 1969	62	Stomatopoda of the western Atlantic	a, k
Manning and Chace 1971	11	Processidae of the northwestern Atlantic	a, k
Perez Farfante 1969	8	Genus <i>Penaeus</i>	a, k
Perez Farfante 1971	5	Genus <i>Metapenaeopsis</i>	a, k
Provenzano 1959	23	Shallow-water hermit crabs of Florida	a, k
Rathbun 1918	238	Grapsoid crabs of America	a, k
Rathbun 1925	273	Spider crabs of America	a, k
Rathbun 1930	349	Cancroid crabs of America	a, k
Rathbun 1937	127	Oxystomatous crabs and allied groups	a, k
Williams 1974b	14	Genus <i>Callinectes</i>	a, k

* NOTE: This is not meant to be exhaustive, but rather a guide to the most accessible literature; earlier references may be omitted if they are covered within the scope of another, more recent treatment. Totals may be approximate to account for supergenera, subspecies, etc.

† Total number of species addressed (includes subspecies and those reviewed from adjacent waters).

‡ Key to contents of papers: a, annotated list; f, faunal list without additional information; k, keys included (or new descriptions).

ORDER DECAPODA
SUBORDER DENDROBRANCHIATA
SUPERFAMILY PENAEOIDEA
Family Penaeidae

Metapenaeopsis martinella Perez Farfante, 1971

Material.—Stations 1, 2, 3 and 5; Sept and May; 10 individuals.

Measurements.—One juvenile male, 10 mm cl; mature females, 9.8 to 12.6.

Habitat.—Chace (1972) reported specimens from coral reefs, shelly bottoms and calcareous algae.

Remarks.—This species was identified in Heck (1977) as *Trachypenaeus restrictus* but reexamination allowed the identification to be corrected. Most individuals from night samples, stations 2 and 3. The species known from Cuba, Brazil, and the western Caribbean; 4 to 137 m. Genus reviewed by Perez Farfante (1971).

Penaeus (Melicertus) duorarum notialis Perez Farfante, 1967

Material.—Stations 1–5; present in all sampled months; 300 individuals.

Measurements.—Males, 3.9 to 6.3 mm cl; females, 4.5 to 20.6.

Habitat.—On muds, sand and sand within rocky patches.

Remarks.—Specimens taken primarily in day trawls (cf. Greening and Livingston 1982); most were immature. Over 80% from station 1. Subspecies ranges from Cuba to the Virgin Islands, Mexico, the Caribbean Sea to Brazil and the western coast of Africa; to 732 m, though generally to 65 m. Genus reviewed by Perez Farfante (1969).

Family Sicyoniidae

Sicyonia laevigata Stimpson, 1871

Material.—Stations 1, 2 and 3; May only; 16 individuals.

Measurements.—Males (two), 7.4 mm cl; mature females, 7.2 to 11.1.

Habitat.—Common in areas with abundant shell cover and among rocks; also in *Thalassia*.

Remarks.—All but two (87%) collected in night samples. Williams (1965) noted sexually mature individuals as small as 18 mm total length. Greening and Livingston (1982) reported *S. laevisata* in their nighttime seagrass samples. Species ranges from North Carolina to northwestern Florida, the West Indies, Colombia and the Pacific coast of Panama; to 90 m.

SUBORDER PLEOCYMATA
INFRAORDER STENOPODIDEA
Family Stenopodidae

Stenopus hispidus (Oliver, 1811)

Material.—Station 3; Sept and May (night); 2 individuals.

Measurements.—Both males, 6.2 and 7.6 mm cl.

Habitat.—Grass flats and areas with coral rubble (Chace 1972).

Distribution.—Widely ranging from Bermuda, central eastern Florida and south Florida to the West Indian region, Surinam, the Red Sea, Japan, southeast Africa, and Hawaii; to 210 m.

INFRAORDER CARIDEA
SUPERFAMILY PALAEMONIDEA
Family Palaemonidae

Leander tenuicornis (Say, 1818)

Material.—Stations 1–3; April and May; 24 individuals.

Measurements.—Males, 4.9 to 5.1 mm cl; ovigerous females, 6.3 to 8.4.

Habitat.—Most often associated with vegetation, *Sargassum*, *Thalassia* and mangroves (Ledoyer 1969; Chace 1972).

Remarks.—Most individuals from station 1. It is distributed in shallow or pelagic waters of all tropical and subtropical seas except those in the extreme eastern Pacific. Only 2 species known in American waters. See Manning (1961) for a comparison of this species with *L. paulensis* (Ortmann).

Periclimenes americanus (Kingsley, 1878)

Material.—Majority at station 1; collections scattered throughout sampling period; 19 individuals.

Measurements.—Males, 2.3 to 3.5 mm cl; ovigerous females, 2.7 to 3.3.

Habitat.—Associated with coral reefs, on mud and sand flats, submerged structures and especially in seagrass and mangrove habitats (Chace 1972).

Distribution.—Species ranges from Bermuda, North Carolina to northwest Florida, Yucatan Peninsula, and West Indies; to 73 m.

Family Gnathophyllidae

Gnathophylloides mineri Schmitt, 1933

Material.—One ovigerous female; data lost.

Measurements.—2.2 mm cl.

Habitat.—Among sea urchin spines, rocks, and coral rubble (Chace 1972).

Distribution.—From Bermuda, southeastern Florida, Yucatan Peninsula and the Caribbean Sea; littoral and sublittoral.

SUPERFAMILY ALPHEOIDEA

Family Processidae

Ambidexter symmetricus Manning and Chace, 1971

Material.—Stations 1, 2 and 3; May; 7 individuals.

Measurements.—Males, 3.4 to 4.3 mm cl; ovigerous females, 3.4 to 5.2.

Habitat.—Common on vegetated bottoms, especially seagrasses.

Remarks.—One individual (5.8 mm cl) was infested with a bopyrid isopod (branchial; Table 2). Processid shrimp are a common seagrass-inhabiting group, being taken especially at night (Ledoyer 1969; Manning and Chace 1971; Greening and Livingston 1982; personal observations). This species is noted from the west-

ern Atlantic, including eastern and western Florida (Gulf of Mexico), Puerto Rico and Trinidad; to 6 m. This is the first report of *A. symmetricus* from Panama.

Processa fimbriata Manning and Chace, 1971

Material.—Most from stations 1 and 2; Apr and May; 55 individuals.

Measurements.—Males, 2.9 to 4.2 mm cl; ovigerous females, 5.4 to 5.6.

Habitat.—Areas of broken shell, coral rubble, sponges and *Thalassia*.

Remarks.—The majority of the individuals collected at night (93%). Reported from North Carolina to Brazil, including south Florida, the Bahamas and Puerto Rico; sublittoral to 37 m. This constitutes a new record for Panama.

Family Alpheidae

Alpheus armillatus H. Milne Edwards, 1837

Material.—Stations 1, 2 and 3; May only; 16 individuals.

Measurements.—Males, 5.3 to 9.2 mm cl; one non-ovigerous female, 11.7; ovigerous females, 5.3 to 11.7.

Habitat.—In oyster bars, coral rubble, rocks and *Thalassia* beds (Chace 1972).

Distribution.—Bermuda, North Carolina to the Gulf of Mexico and Brazil; sublittoral.

Alpheus floridanus Kingsley, 1878

Material.—Stations 1 and 2; Oct, Dec and Jan; 8 individuals.

Measurements.—Males, 4.3 to 8.8 mm cl; ovigerous females, 6.4 to 19.8.

Habitat.—Soft-sediments.

Distribution.—From Bermuda, the southeastern United States to the Gulf of Mexico, Brazil, Guyana and the Congo (eastern Atlantic); to 37 m.

Alpheus formosus Gibbes, 1850

Material.—Stations 1 and 3; Aug and Mar; 2 females.

Measurements.—3.6 and 5.5 mm cl.

Habitat.—On sand and mud flats, rocks, oyster bars and coral rubble.

Distribution.—From Bermuda, North Carolina and throughout the West Indies to Brazil; to 42 m.

Alpheus normanni Kingsley, 1878

Material.—Stations 1 and 5; Oct and May; 4 individuals.

Measurements.—Males, 4.1 to 5.4 mm cl; one ovigerous female, 6.3.

Habitat.—In *Thalassia*, sponges and coral rubble (especially *Porites*); also among ascidians (Abele 1970).

Remarks.—All 3 males were found associated with a sponge (Station 5). Wass (1955) found this shrimp to be common in the northeast Gulf of Mexico, and Greening and Livingston (1982) collected this species mostly at night. Found from Bermuda, Virginia to the Gulf of Mexico, throughout the West Indies to Tobago and in the Pacific in the Gulf of California; littoral to 73 m.

Synalpheus fritzmuelleri Coutière, 1909

Material.—Stations 1 and 2; Aug, Feb and May; 6 individuals.

Measurements.—Ovigerous females (two), 3.2 and 5.0 mm cl; remaining specimens, 2.9 to 3.8.

Habitat.—Commonly collected in sponges (Abele 1970) and in grass flats, as well as among mangrove roots (Chace 1972).

Remarks.—Both ovigerous females collected from sponges. *S. fritzmuelleri* recorded from Bermuda, North Carolina to the Gulf of Mexico and the West Indies to Brazil; in the eastern Pacific from Baja, California; littoral to 50 m.

Synalpheus goodei Coutière, 1909

Material.—Station 2; Oct; 19 individuals.

Measurements.—Ovigerous females (13), 4.6 to 6.1 mm cl.

Habitats.—Associated with rocky intertidal areas encrusted with corals; Gore (pers. comm.) found it living on or near a large keratose sponge.

Remarks.—Six of the 19 specimens lost in transit. Species known from Bermuda, central east Florida Gore (pers. comm.), the Gulf of Mexico and Curaçao; to 60 m.

Synalpheus pandionis Coutière, 1909

Material.—Stations 1 and 2; Aug and Feb; 3 individuals.

Measurements.—Ovigerous females (three), 4.9 to 5.5 mm cl.

Habitat.—Collected from *Thalassia* with clumps of *Porites* rubble and algae (Chace 1972).

Distribution.—This rare species reported from the Gulf of Mexico, Barbados and Curaçao; to 60 m.

Synalpheus townsendi Coutière, 1909

Material.—Station 2; Aug and Feb; 4 individuals.

Measurements.—One ovigerous female, 4.0 mm cl; the remaining specimens, 1.9 to 3.9.

Habitat.—Common in sponges (Abele 1970) and *Thalassia* beds with clumps of *Porites* (Chace 1972). Gore (1981) recorded it from a deep reef in the Florida Keys.

Remarks.—Chace (pers. comm.) suggests that references to associations with *Pocillopora* are in error, referring probably to growth forms of *Porites*. Species occurs from Bermuda and North Carolina, southwest through the Gulf of Mexico and the West Indies to Brazil; to 102 m.

Family Hippolytidae

Hippolyte zostericola (Smith, 1873)

Material.—Stations 2 and 3; Sept and May; 4 individuals.

Measurements.—Four ovigerous females, 1.7 to 2.6 mm cl.

Habitat.—Usually common in submerged vegetation (Chace 1972; Greening and Livingston 1982).

Remarks.—From Bermuda and Massachusetts to the Yucatan Peninsula, Trinidad and Curaçao; in shallow waters. See Williams (1965) and Chace (1972) for a discussion of its taxonomic difficulties.

Latreutes fucorum (Fabricius, 1798)

Material.—Stations 1 and 2; Apr and May; 15 individuals.

Measurements.—Ovigerous females, 2.3 to 3.5 mm cl; a single non-ovigerous female, 2.2.

Habitat.—Most often associated with floating and submerged vegetation (Wass 1955; Abele 1970; Chace 1972).

Distribution.—Ranges from Newfoundland to the Gulf of Mexico, Bermuda and Puerto Rico; pelagic (in vegetation) and sublittoral.

Thor manningi Chace, 1972

Material.—Stations 1, 2 and 5; Aug and May; 12 individuals.

Measurements.—Single male, 2.3 mm cl; ovigerous females, 1.9 to 3.7; females (non-ovigerous), 1.8 to 2.6.

Habitat.—Common in grass flats.

Remarks.—Most specimens were taken in night samples. Recorded from Bermuda, North Carolina to Tobago, Curaçao and in the eastern Pacific; to 4 m. Chace (1972) suggested that this hippolytid may be a sequential (protandric) hermaphrodite.

Tozeuma carolinense Kinglsey, 1878

Material.—Stations 1–5; all months sampled; 1068 individuals.

Measurements.—Males (mature), 3.5 to 6.7 mm cl; ovigerous females, 5.1 to 10.8; non-ovigerous females, 5.2 to 9.4. Several males less than 3.5 mm cl were collected, each with a developing appendix masculina.

Habitat.—Common in vegetation, with color being highly variable (Abele 1970; Greening and Livingston 1982; pers. obs.).

Remarks.—*T. carolinense* dominated with decapoda fauna (ranked by abundance) at all stations. Ovigerous females were found throughout the year, with ovigery in a given collection always greater than 65%. Previous studies on this species have been primarily concerned with its larval development (Bryce 1961; Ewald 1969), although Voss (1956) briefly discussed its natural history. Found from Bermuda and Massachusetts to Panama; littoral to 75 m.

Trachycaris restrictus (A. Milne Edwards, 1878)

Material.—Stations 2, 3 and 5; Aug, Mar, Apr and May; 13 individuals.

Measurements.—Ovigerous females (13), 5.0 to 6.8 mm cl.

Remarks.—Genus with one species. This rare and curious looking hippolytid has been recorded from Bermuda to Brazil and in the eastern Atlantic from Canary Islands to Saint Helena Island (Holthuis 1949); to 100 m. This is probably the first record of this species from Panama.

INFRAORDER PALINURA
SUPERFAMILY PALINUROIDEA
Family Scyllaridae

Scyllarus Fabricius, 1775

Remarks.—Two individuals were collected; however, both were lost in transit. See Williams (1965) and Lyons (1970) for a review of this group.

Family Palinuridae

Palinurus argus (Latreille, 1804)

Material.—Stations 1, 2 and 5; Aug, Oct, Mar, Apr and May; 27 juvenile individuals.

Measurements.—Specimens ranged from 11.2 to 37.4 mm cl.

Habitat.—Spiny lobsters commonly found around rocky and coral reef areas; generally in areas offering concealment (Khandler 1964; Davis 1971, 1981; Berrill 1975).

Remarks.—Juveniles were taken primarily at Station 1, possibly associated with the nearby red mangroves, where dense prop roots offer areas of concealment (Heck 1977). *P. arsus* has been recorded from Bermuda, North Carolina to the Gulf of Mexico, the West Indies and Brazil; to 100 m. Williams (1965) gives a general overview of this species' ecology.

INFRAORDER ANOMURA
SUPERFAMILY COENOBITOIDEA

(Note: hermit crabs were tentatively identified in Panama by one of us (KLH); however, most were damaged during extraction. Though intact specimens were originally verified, measurements and sexing for most specimens were impossible).

Family Diogenidae

Calcinus tibicen (Herbst, 1791)

Material.—Stations 2, 3 and 5; Sept and May night; 3 individuals.

Measurements.—One specimen measured, 4.4 mm sl.

Habitat.—Common in rocky shores.

Remarks.—Found in Bermuda, the West Indies, Florida and Brazil; intertidal to 32 m. See Provenzano (1959) for further information.

Clibanarius antillensis Stimpson, 1862

Material.—Stations 1–5; all sampled months; 91 individuals.

Measurements.—Measurable specimens from 1.6 to 4.7 mm sl.

Remarks.—Ovigerous females were present in August and September. Over 68% of the specimens from station 2. Known from Bermuda, south Florida, the West Indies, Curaçao and Brazil; in shallow waters. See Provanzano (1959) for additional information.

Dardanus venosus (H. Milne Edwards, 1848)

Material.—Stations 2, 3 and 5; Aug, Apr and May; 3 individuals.

Measurements.—One male, 6.4 mm sl; two females, 8.3 and 16.1.

Habitat.—Found in grassbeds (Williams 1965).

Remarks.—Bright red transverse bands on walking legs and chela make this species quite distinctive, even after alcohol preservation. Found from North Carolina to the West Indies, including Surinam, Brazil and Bermuda. Found near-shore to 91 m, but has been collected to 366 m. Biffar and Provenzano (1972) treat this species in their review of the genus.

Paguristes limonensis McLaughlin and Provenzano, 1974

Material.—Stations 1–5; all sampling months; 166 individuals.

Measurements.—Males, 3.3 to 3.6 mm sl; measured females (all ovigerous), 3.6 to 5.9.

Remarks.—Over 77% of these hermit crabs were collected at night. The majority of individuals were badly damaged during extraction from the shell. Ovigerous females were taken in July, August, September, November, January, March, April and May. This recently described species ranges from the west coast of Florida, Panama and Colombia; to 234 m. See McLaughlin and Provenzano (1974) for a more detailed taxonomic discussion.

SUPERFAMILY PAGUROIDEA

Family Paguridae

Pagurus bonairensis Schmitt, 1936

Material.—Stations 1–5; all months sampled; 190 individuals.

Measurements.—Ovigerous females, 3.1 to 4.8 mm sl.; remaining specimens, 2.4 to 5.2.

Habitat.—Common in seagrass (*Thalassia*) beds (in the northeastern Gulf of Mexico, Abele 1970; Greening and Livingston 1982; personal obs.).

Remarks.—Most individuals collected at station 4; over 26% were collected in May night trawls. Ovigerous months included July, August, September, November, March and May. This abundant species was previously misidentified as *P. annulipes* (see Rouse 1970) by Provenzano (1959). Occurs in Florida, Cuba and Puerto Rico, although in the northern part of its range this species is often confused with *P. annulipes* (Rouse 1970; García-Gómez 1982). García-Gómez (1982) provides further clarification.

Pagurus brevidactylus (Stimpson, 1858)

Material.—Stations 1–5; all sampling months; 50 individuals.

Measurements.—Ovigerous females, 3.9 to 5.4 mm sl; remaining intact specimens, 3.6 to 4.1.

Habitat.—Provenzano (1959) suggests that this species is most often taken on hard bottoms to 229 m; we collected our samples in sandy-vegetated areas less than 2 m.

Remarks.—Ovigerous months included August, September and February to May. This species has been noted from Bermuda, Florida, the Caribbean and northeast Gulf of Mexico; intertidal to 50 m. See McLaughlin (1975) and Lemaitre *et al.* (1982) for a reclarification of this species.

SUPERFAMILY GALATHEOIDEA

Family Porcellanidae

Megalobrachium mortenseni Haig, 1962

Material.—One individual; all additional data lost.

Measurements.—Male, 4.0 mm cw.

Habitat.—In sandy areas with calcareous algae (Brazil), coarse sediments (gravel) and among rocks.

Remarks.—Haig (1962) discussed the close resemblance of *M. mortenseni* to *M. erosum*, the latter occurring in the Gulf of California. Gore and Abele (1976) considered the two to be geminate species. Reported from the Virgin Islands southward to Brazil; to 27 m. This is a new record for Caribbean Panama.

Petrolisthes armatus (Gibbes, 1850)

Material.—Stations 1, 2 and 3; Aug to Mar; 38 individuals.

Measurements.—Male, 3.8 to 7.4 mm cw; ovigerous females, 3.0 to 6.3; non-ovigerous females, 3.1 to 4.3.

Habitat.—Found in oyster and mussel bars, coral rubble, mangroves and around pilings (Haig 1960). Gore and Abele (1976) found this species abundant in rocky coralline intertidal on both sides of the Panamanian isthmus.

Remarks.—Ovigerous females found in all collecting months. Haig (1960) reports ovigerous females also throughout the year among material examined from intertidal and subtidal habitats. This porcellanid crab is reported from Bermuda, Georgia and central eastern Gulf coast of Florida to Brazil; western Africa and eastern Pacific (Gulf of California to Peru); to 20 m.

Petrolisthes galanthinus (Bosc, 1802)

Material.—Stations 1, 2, 3 and 5; July to May; 44 individuals.

Measurements.—Males, 3.6 to 7.0 mm cw; ovigerous females, 4.4 to 8.8; a single non-ovigerous female, 4.1.

Habitat.—Under rocks, coral rubble and on shell and sand bottoms. Also associated with sponges, coral and anenomes (Haig 1960; Gore and Abele 1976).

Remarks.—Ovigerous females were taken July, August, February and March (September and October were the only other months when females were taken at all). Haig (1960) found ovigerous females in January, February and March; southwest Caribbean, ovigery from January to August (Gore and Abele 1976). Species common in the Atlantic from North Carolina to Brazil, including the Caribbean area and Surinam. In the Pacific, Haig (1960) reported it only from Panama, but Gore and Abele (1976) noted its occurrence from Ecuador and Costa Rica also.

INFRAORDER BRACHYURA
SECTION DROMIACEA
SUPERFAMILY DROMIOIDEA
Family Dromiidae

Dromidia antillensis Stimpson, 1858

Material.—Station 3; Apr; 2 individuals.

Measurements.—Males (two), 17.8 and 18.8 mm cw.

Habitat.—Most often on rocky substrates.

Remarks.—These crabs typically carry sponges or tunicates with their fifth leg, modified for grasping the dorsal covering; both specimens had sponges. Found from Bermuda and North Carolina to the Gulf of Mexico, the West Indies, Colombia and Surinam to Brazil; littoral to 300 m. See Powers (1977) for an excellent summary of this group.

SECTION OXYSTOMATA
SUPERFAMILY LEUCOSIOIDEA
Family Calappidae

Calappa angusta H. Milne Edwards, 1880

Material.—Stations 1 and 2; Aug, Nov, Mar and May; 4 individuals.

Measurements.—Males (four), 6.3 to 45.1 mm cw (45.1 mm, mature).

Habitat.—From coral, sand, shell and gravel substrates.

Distribution.—From Bermuda and North Carolina to Brazil, including the West Indies and the Gulf of Mexico; to 200 m.

Calappa ocellata Holthuis, 1958

Material.—Stations 1 and 2; both were lost in transit; 2 individuals.

Habitat.—Among corals and on sandy bottoms.

Remarks.—This and the previous calappid species possess a large, toothed dactyl used to open gastropod shells (often with hermits inside, Vermeij 1982). Shoup (1968) discusses this unique predatory behavior. *C. ocellata* ranges from Bermuda and North Carolina to Brazil; to 52 m, though common in shallower waters (see Holthuis 1958).

Hepatus pudibundis (Herbst, 1785)

Material.—Station 1; specimens lost; 2 individuals.

Habitat.—On sand, mud and shelly bottoms (Holthuis 1959).

Remarks.—The low abundance of this and the previous two calappid species is surely a result of their habit of remaining partially buried much of the time (Pearse, Humm and Wharton 1942), thus escaping collection by trawling. This species has been reported from North Carolina to Brazil, including Louisiana and Texas in the Gulf of Mexico and from western Africa; intertidal to 49 m.

SECTION OXYRHYNCHA
SUPERFAMILY MAJOIDEA
Family Majidae

Chorinus heros (Herbst, 1790)

Material.—Stations 1, 2 and 3; May night; 6 individuals.

Measurements.—One male, 11.3 mm cw; females, 10.7 to 17.0.

Habitat.—Found on rocks, broken shell, coarse sand, sponges, and sabellarid reefs (Gore, pers. comm.).

Distribution.—From Bermuda and central eastern Florida to Cuba and Brazil; shallow to 48 m.

Macrocoeloma diplacanthum (Stimpson, 1860)

Material.—Stations 1–5; all collecting months; 33 individuals.

Measurements.—Males from 7.4 to 31.8 mm cw (including lateral spines); non-ovigerous females, 16.9 to 28.7; ovigerous females, 21.8 to 28.4.

Habitat.—Near shallow reefs and on sandy substrates.

Remarks.—All individuals were collected in day sampling. Ovigerous females found in July, August, November and April. Animals were always encrusted with numerous sponges, algae and debris. Rathbun (1925) reported individuals from Jamaica and Cuba with rhizocephalan infestations, but none were found infested here. Species ranges from Key West, Florida to Colombia, including the Bahamas and the Caribbean Sea; in shallow water to 24 m.

Microphrys bicornutus (Latrielle, 1825)

Material.—Stations 1–5; all months sampled; 195 individuals.

Measurements.—Mature males, 5.1 to 23.3 mm cw (including lateral spines); immature males, 8.8 to 8.9; mature females, 6.2 to 17.6; immature females, 6.3 to 8.9; ovigerous females, 11.6 to 21.1.

Habitat.—On reefs, seagrasses, sponges, and a variety of substrates such as shell, rock, sand and mud.

Remarks.—This majid ranked third in overall species abundance. It was most common at stations 1 and 2. Twenty-six ovigerous females were collected (in all months but March). These “decorator crabs” covered with a variety of algae, sponges and other sessile invertebrates. *M. bicornutus* occurs from North Carolina to Brazil, including the Bahamas, the Florida Keys, St. Croix (pers. obs.), Colombia and Bermuda; to 30 m. Powers (1977) provides an excellent review of this species. Williams (1965) summarizes its known parasites and Hazlett (1979 and included references), the behavioral literature on this species. This is one of the few species dealt with here, whose biology has been studied in some detail.

Mithrax (Mithraculus) forceps (A. Milne Edwards, 1875)

Material.—Stations 1–5; in all sampling months; 88 individuals.

Measurements.—Males, 4.9 to 21.2 mm cw; ovigerous females (17), 6.8 to 16.4; non-ovigerous females, 6.8 to 16.4.

Habitat.—Under coral rubble, in sponges, *Thalassia* beds, and several coarse substrates (coral, shell, and rock).

Remarks.—Most (87%) were collected during daytime trawls. Ovigerous females were found from July to October, January and March to May (all months within which females were collected). Abele (1970) noted that this brick red crab commonly preyed on barnacles. Recorded from Bermuda, North Carolina to the Gulf of Mexico, Trinidad and Colombia; intertidal to 90 m. See Powers (1977) for a brief introduction to this species' biology.

Mithrax (Mithraculus) ruber (Stimpson, 1871)

Material.—Station 4; data lost; 1 individual.

Habitat.—From sand, coral and mud substrates, with sponges and in seagrasses near reefs.

Distribution.—Puerto Rico, Cuba, St. Thomas, Barbados, Curaçao and Colombia; to 153 m, though usually shallower.

Pitho Bell, 1835

Remarks.—A total of 148 individuals belonging to this genus were collected over the course of this study. Over 70% were from May night trawls. In daytime sampling, most (70%) individuals at station 1; for night samples, the majority (60%) at station 3 (May). No *Pitho* spp. were taken at station 2 (daytime), yet 19 individuals (most *P. lherminieri*) were collected at night (May).

The following account by species, for the genus *Pitho* is tentative. We found, and others have noted (Abele 1970 and pers. comm.), a great deal of variation (especially with size and sex) regarding the lateral teeth of the carapace. Rathbun's (1925) key to the species employs these teeth as major diagnostic characters. Based on our observations of over 140 individuals, other criteria must be used to sort out specimens to species, particularly when several are sympatric. Rathbun (1925) has some excellent figures (fig. 116 and 117) of both male abdominal segments and antennal articles, but caution should be exercised when crabs are immature or adults are larger than average-sized. Note: totals below may be different than original species counts (Heck 1977); some specimens were lost.

Pitho aculeata (Gibbes, 1850)

Material.—Stations 1 and 3; Aug, Sept and Mar to May; 9 individuals (tentatively identified).

Measurements.—Mature males, 10.6 to 24.6 mm cw; juvenile males, 12.1 to 14.4; one ovigerous female, 19.3; mature females (non-ovigerous), 20.6 to 22.4; one juvenile female, 12.9.

Habitat.—Sand, shell and mud bottoms with corals; algae (e.g. *Sargassum*) and seagrass.

Remarks.—All were collected in daytime sampling. Reported from the Bahamas, Florida (west and Keys) to the West Indies and the northern coast of South America; in shallow water.

Pitho anisodon (von Martens, 1872)

Material.—Stations, 1–4; Sept, Oct and May; 62 individuals originally identified.

Measurements.—Mature males, 18.1 to 25.3 mm cw; one immature male, 12.4 (May); ovigerous females, 23.7 to 26.8 (all May); one immature female, 10.1 (May); one non-ovigerous female, 26.3 (May).

Habitat.—Found in rocks, sand, grassbeds, mud and coral bottoms.

Remarks.—This species was the most abundant *Pitho* spp. Collected in greatest numbers in September, October and May, with the majority (81%) taken at night in May (37 of 50 at station 3 for all night samples). The species occurs in the Bahamas, Florida, Cuba, Jamaica and Curaçao; to 22 m.

Pitho lherminieri (Schramm, 1867)

Material.—Stations 1–4; all months sampled; 59 individuals originally identified.

Measurements.—Mature males, 12.3 to 22.9 mm cw; juvenile males, 10.5 to 13.5; ovigerous females (two), 16.8 and 18.3 (station 3, May night); non-ovigerous females (mature), 18.3 to 24.9; immature females, 9.5 to 9.8 (September and May).

Habitat.—Found on most coarse bottoms and with seagrasses (Lemaitre 1981); infrequently on mud.

Remarks.—Majority of individuals collected at night in May (63%). Noted from North Carolina to west Florida, the West Indies to Brazil; to 221 m, though usually to 51 m.

Pitho quadridentata (Miers, 1879)

Materials.—Stations 1–4; most in Sept and May; 24 individuals originally identified.

Measurements.—Mature males, 11.5 to 25.0 mm cw; one immature male, 13.0 (May); 4 ovigerous females (Sept and May night), 20.2 to 26.2; juvenile females, 9.5 to 9.8 (Sept and May night).

Remarks.—Most individuals from station 1 (62%). Rathbun (1925) discussed its resemblance to *P. anisodon*. Previously reported only from Jamaica. This probably constitutes the first record for Panama and Central America.

Pitho sexdentata Bell, 1835

Material.—Station 2 night; May; 2 individuals.

Remarks.—Two specimens originally recorded by Heck (1977). This species has previously been collected in the Pacific only (Rathbun 1925; Garth 1958). Unfortunately, these specimens could not be relocated.

Podochela gracilipes Stimpson, 1871

Material.—Stations 1, 3 and 5; May; 3 males.

Measurements.—Males, 3.3 to 4.5 mm cw.

Habitat.—Associated with rocks, gravel, sand, shell and coral.

Distribution.—From North Carolina to the Gulf of Mexico, the Caribbean Sea, including Colombia, Surinam and Brazil; to 220 m, although we collected from depths less than 2 m.

Podochela riisei Stimpson, 1860

Material.—Stations 1 and 3; Aug, Oct and Apr; 4 individuals.

Measurements.—Males, 4.8 to 6.4 mm cw; a single ovigerous female, 9.7 (Apr).

Habitat.—Found on most coarse substrates, though often with algae (e.g. *Sarassum*) and *Thalassia* (Wass 1955; Greening and Livingston 1982).

Remarks.—Abele (1970) found this species often covered with bryozoans. It is reported from Bermuda and North Carolina to Mexico and Brazil; shallow to 90 m.

Podochela sidneyi Rathbun, 1924

Material.—Station 1; Aug, Feb and May; 3 badly damaged individuals.

Distribution.—North Carolina, east and west Florida, Texas, Yucatan Peninsula and Cuba; to 186 m.

[Note: these 3 *Podochela* spp. are very similar and the identifications are all tentative; dactyls of the last 3 legs missing). Wass (1955) suggests that *P. sidneyi*'s sternal plates are flatter than those of *P. riisei*.]

Stenorhynchus seticornis (Herbst, 1788)

Materials.—Stations 3, 4 and 5; Aug to Nov; 9 individuals.

Measurements.—Males, 9.8 to 18.7 mm cw; two ovigerous females (September), 10.0 and 10.7; non-ovigerous females, 7.7 to 9.7.

Habitats.—On coarse bottoms such as rock, gravel, sand, shell and coral rubble.

Remarks.—Found from Bermuda, North Carolina to Brazil, including Colombia; to 1487 m, though more often in shallower waters. Yang (1967) recognized three distinct species in the Atlantic. Previous accounts of *S. seticornis* from the eastern Atlantic (West Africa) are incorrect. Manning and Holthuis (1981:304) review the current status of this genus in the Atlantic. Powers (1977) briefly lists references on the biology of this interesting crab. See Schnever (1978) for some recent work on this species.

SUPERFAMILY PARTHENOPOIDEA

Family Parthenopidae

Heterocrypta granulata (Gibbes, 1850)

Material.—Station 4; August; one individual.

Measurements.—Male, 12.8 mm cw.

Habitat.—Found on shelly, mud, sand, gravel, rock and coral bottoms; also collected in *Thalassia* (Lemaitre 1981).

Remarks.—This parthenopid crab has been reported from Massachusetts to Georgia, the Gulf of Mexico, and the West Indies to Brazil; generally less than 50 m. Gore and Scotto (1979) provide an excellent review of the family.

SECTION BRACHYRHYNCHA
SUPERFAMILY PORTUNOIDEA
Family Portunidae

Callinectes danae Smith, 1869

Material.—Stations 1–5; all sampling months; 66 individuals.

Measurements.—Mature males, 58.3 to 105.4 mm cw (including lateral spines); juvenile males, 20.4 to 69.4; ovigerous females (two), 76.4 and 99.2; females (mature), 61.9 to 103.6; juvenile females, 20.9 to 60.3.

Habitat.—Common in muddy estuaries, in mangroves, algae, and shelly bottoms; from nearly fresh to full strength seawater (Williams 1974b).

Remarks.—Ovigerous females taken in August and October. Miles (1951) reported ovigerous females beginning at 67 mm cw. Rathbun (1930) found *C. danae* along high energy sandy beaches and Park (1969) noted its occurrence on the seaward sides of islands in Biscayne Bay, Florida. Over 38% of the crabs maintained a rhizocephalan infection (Table 2). This species noted from Bermuda, Central Florida and the Yucatan Peninsula to Brazil; to 75 m. Williams (1974b) reviews this genus.

Cronius tumidulus (Stimpson, 1871)

Material.—Stations 1, 2, 3 and 4; 93% in May (night); 59 individuals.

Measurements.—Mature males, 15.0 to 35.2 mm cw (including lateral spines); juvenile males, 9.0 to 15.5 (May); two ovigerous females (Station 2 and 3, May night); mature females, 16.1 to 34.2 (Sept and May); juvenile females, 9.3 to 14.0 (May only).

Habitat.—Coral, sand and rocky bottoms and in *Sargassum* and *Thalassia*.

Remarks.—This species has often been reported from *Thalassia* beds (Rathbun 1930; Garth 1978); in fact, Park (1969) found it exclusively there. Several crabs had rhizocephalans (see Table 2). Noted from Bermuda, the central east and west coasts of Florida, the Florida Keys and the Bahamas; 73 m.

Lupella forceps (Fabricius, 1793)

Material.—Station 3; Dec; one individual.

Measurements.—One immature male, 30.5 mm cw (including lateral spines).

Habitat.—Common offshore on muddy bottoms and in vegetated areas (Park 1969).

Distribution.—Found in the West Indies, Colombia and Surinam; Parks (1969) collected one individual in Biscayne Bay, Florida; to 15 m.

Portunus ordwayi (Stimpson, 1860)

Material.—Stations 1 and 2; May night; 10 individuals.

Measurements.—Males, 42.8 to 48.8 mm cw (including lateral spines), ovigerous females (two; station 1 May night), 40.7 and 46.0; females (non-ovigerous), 40.6 to 45.4.

Habitat.—On sand, gravel, shell and coral rubble bottoms.

Distribution.—From Massachusetts, Bermuda and North Carolina to the Gulf of Mexico, the Caribbean Sea and southward to Brazil; to 106 m.

SUPERFAMILY XANTHOIDEA

Family Goneplacidae

Cyrtoplax spinidentata (Benedict, 1892)

Material.—Stations 1 and 3; Dec, Jan and May; 3 individuals.

Measurements.—Males (three), 9.9 to 16.8 mm cw.

Habitat.—With sponges and algae.

Remarks.—This monospecific genus previously known from the West Indies (Jamaica, Puerto Rico, St. Thomas and Trinidad); in shallow water. This constitutes the first record for Panama and Central America.

Family Xanthidae

Panopeus occidentalis Saussure, 1857

Material.—Stations 1–5; all months sampled; 96 individuals.

Measurements.—Males, 4.0 to 30.5 mm cw; females, 6.0 to 28.8.

Habitats.—On sand, shell, rock and gravel bottoms, around sponges, mangrove roots, pilings; in *Thalassia* (and algae) in the Bahamas (Garty 1978) and Colombia (Lemaitre 1981).

Remarks.—Most specimens from station 1 (65%) in day trawls 88%; see also observations by Oliveira (1940). Oviparous females in July, September, and October. This abundant xanthid ranges from Bermuda, North Carolina to Brazil including the West Indies; intertidal to 18 m. Williams (1965) provides a synopsis on the biology of this species.

Pilumnus dasypodus Kingsley, 1879

Material.—Station 5; Aug; one individual.

Measurements.—One ovigerous female, 7.5 mm cw.

Habitat.—Reported on sponges from pilings, jetties and buoys (Abele 1970).

Remarks.—Ranges from North Carolina to the Gulf of Mexico, and the West Indies to Brazil including Colombia; to 29 m. Williams (1965) has summarized the ecology of this species. (Note: two other *Pilumnus* were originally identified [KLH] in Panama as *P. reticulatus* Stimpson [2 specimens] and *P. pannosus* Rathbun [9 specimens]; however, these were lost in transport).

Discussion

Of the 58 decapod species discussed here, five or 8.6% represent new records for Caribbean Panama and of these, one (*Cyrtoplax spinidentata*), represents a new record for Central America. Both of the two stomatopod species were previously known from Central American waters. No endemics were found.

Although our collection is only a small percentage of the total decapod fauna of Panama (estimated to be 1400 species by Abele [1972]), we believe that we have good coverage of the grassbed fauna. Those species missed will be mostly infaunal, such as alpheid and stomatopods, or rare species, especially those active at night.

The species treated here show close affinities with the Carolinian fauna treated by Williams (1965). For example 34 (59%) of the species collected in Panama

Table 2.—Summary of parasitic infestations during 1974–75 sampling period.

Species infested	# of individuals*	Pertinent data
<i>Ambidexter symmetricus</i>	1	1 ♀, 5.8 mm cl; Station 1 May
<i>Callinectes sapidus</i>	17	17 ♀, 53.9–91.8 mm cw Aug, Sept, Oct, Dec, Feb Mar, Apr, May; Stations 1, 2, 3, & 5
<i>Cronius tumidulus</i>	2	1 ♂, 1 ♀, 15.8, 18.2 mm cw Aug and May; Stations 1 and 2
<i>Microphrys bicornutus</i>	3	2 ♂, 1 ♀, 8.3–9.1 mm cw Oct, Mar and May; Stations 1, 2 & 3
<i>Panopeus occidentalis</i>	1	1 ♀, 8.8 mm cw Aug, Station 1

* Note: Rhizocephalan occurrences for all species except *A. symmetricus*. One processid with bopyrid isopod (branchial).

grassbeds are also found off the Carolinas (Williams 1965). Thirty-seven (64%) of our species are known from Bermuda (Markham and McDermott 1981). Most of our species are, however, restricted to tropical, subtropical and warm temperate waters. This is exemplified by the fact that only two of our species (3.4%) show up on Williams (1974a) check list of the decapods of the northeastern United States (New Jersey to Maine). In addition 14 species (24%) are shared with the results of Heck's (1979) trawling study in turtlegrass beds of the northwestern Gulf of Mexico, while only two species (3.4%) are shared with the decapods collected in a similar trawling study in eelgrass beds of the lower Chesapeake Bay (Heck and Orth 1980).

Acknowledgments

We thank L. G. Abele, R. H. Gore, and F. A. Chace, Jr. for their constructive criticisms of earlier drafts of the paper. Species identifications were gladly given by Drs. Lawrence G. Abele, Florida State University (Decapods) and Patsy McLaughlin, Florida International University (hermit crabs). Support for this work was provided by the Department of Biological Science (Florida State University), the Department of Zoology (University of Maryland), by a Smithsonian Predoctoral Fellowship to one of us (KLH) and by the Division of Environmental Research, Academy of Natural Sciences of Philadelphia.

Literature Cited

- Abele, L. G. 1970. The marine decapod (Crustacea of the northwestern Gulf of Mexico.—M.S. thesis, Florida State University, Tallahassee, 137 pp.
- . 1972a. Comparative habitat diversity and faunal relationships between the Pacific and Caribbean decapod Crustacea of Panama.—Ph.D. dissertation, University of Miami, Florida 124 pp.
- . 1972b. Comparative habitat diversity and faunal relationships between the Pacific and Caribbean Panamanian decapod Crustacea: a preliminary report with some remarks on the crustacean fauna of Panama.—Bulletin of the Biological Society of Washington 2:125–138.
- , and N. Blum. 1977. Ecological aspects of the freshwater decapod crustaceans of the Perlas Archipelago, Panamá.—Biotropica 9:239–252.

- , and B. E. Felgenhauer. 1982. Decapoda.—In: S. P. Parker, ed., *Synopsis and classification of living organisms*, Volume 2, pp. 296–326. McGraw-Hill, New York.
- Berrill, M. 1975. Gregarious behavior of the spiny lobster, *Panulirus argus* (Crustacea, Decapoda).—*Bulletin of Marine Science* 25:515–522.
- Biffar, T. A., and A. J. Provenzano, Jr. 1972. Biological results of the University of Miami Deep-Sea expeditions. 94. A reexamination of *Dardanus venosus* (H. Milne Edwards) and *D. imperator* (Miers), with a description of a new species of *Dardanus* from the western Atlantic (Crustacea, Decapoda, Diogenidae).—*Bulletin of Marine Science* 22:775–805.
- Bowman, T. E., and L. G. Abele. 1982. Classification of the recent Crustacea.—In: L. G. Abele (ed.) *The Biology of Crustacea*, pp. 1–28, Academic Press, New York.
- Bryce, G. W., Jr. 1961. Larval development of *Tozeuma carolinense* Kingsley, including ecological notes on adults.—M.S. thesis, University of North Carolina, Chapel Hill, North Carolina 59 pp.
- Camp, D. K. 1973. Stomatopod Crustacea.—*Memoirs of the Hourglass Cruises*, Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida 3(2), 100 pp.
- Chace, F. A., Jr. 1972. The shrimps of the Smithsonian-Bredin Caribbean Expeditions, with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia).—*Smithsonian Contributions to Zoology* 98, 179 pp.
- Coutière, H. 1909. The American species of snapping shrimps of the genus *Synalpheus*.—*Proceedings of the U.S. National Museum* 36:1–93.
- Davis, G. E. 1971. Aggregations of spiny sea urchins, *Diadema antillarum*, as shelter for young spiny lobsters, *Panulirus argus*.—*Transactions of the American Fisheries Society* 100:586–587.
- . 1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management.—*Fishery Bulletin* 78:979.
- Ewald, J. J. 1969. Observations on the biology of *Tozeuma carolinense* (Decapoda, Hippolytidae) from Florida, with special reference to larval development.—*Bulletin of Marine Science* 19:510–549.
- Felder, D. L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico.—Publication No. LSU-56-73-02 of the Center for Wetland Resources, L.S.U., Baton Rouge, Louisiana. 103 pp.
- García-Gómez, J. 1982. The Provenzanoid group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic Part I. *Pagurus naclaughlinae*, a new species.—*Bulletin of Marine Science* 32:647–655.
- Garth, J. S. 1948. The Brachyura of the “Askoy” Expedition with remarks on carcinological collecting in the Panama Bight.—*Bulletin of the American Museum of Natural History* 92(1):1–66.
- . 1958. Brachyura of the Pacific coast of America, Oxyrhyncha.—*Allan Hancock Pacific Expeditions*. 21(1):1–499.
- . 1978. Marine biological investigations in the Bahamas. 19. Decapoda Brachyura.—*Sarsia* 63:317–333.
- Glynn, P. W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama.—*Bulletin of the Biological Society of Washington* 2:13–30.
- Gore, R. H. 1981. Three new shrimps, and some interesting new records of decapod Crustacea from a deep-water coral reef in the Florida Keys.—*Proceedings of the Biological Society of Washington* 94(1):135–162.
- . 1982. Porcellanid crabs from the coasts of Mexico and Central America (Crustacea: Decapoda: Anomura).—*Smithsonian Contributions to Zoology* 363:1–34.
- , and L. G. Abele. 1976. Shallow water porcelain crabs from the Pacific and adjacent Caribbean waters (Crustacea: Anomura: Porcellanidae).—*Smithsonian Contributions to Zoology* 237, 30 pp.
- , and L. E. Scotto. 1979. Crabs of the family Parthenopidae (Crustacea: Brachyura: Oxyrhyncha) with notes on specimens from the Indian River region of Florida.—*Memoirs of the Hourglass Cruises*, Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida 3(6):98 pp.
- Greening, H. S., and R. J. Livingston. 1982. Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities.—*Marine Ecology Progress Series* 7:137–156.
- Haig, J. 1960. The Porcellanidae (Crustacea, Anomura) of the eastern Pacific.—*Allan Hancock Pacific Expeditions* 24:1–440.

- . 1962. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916 LXXIX: Porcellanid crabs from Eastern and Western America.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 124:171–192.
- Hazlett, B. A. 1979. Individual distance in Crustacea, III. The spider crab *Microphrys bicornutus*.—Zeitschrift für Tierpsychologie 49:65–70.
- Heck, K. L., Jr. 1977. Comparative species richness, composition, and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panama).—Marine Biology 41:335–348.
- . 1979. Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows.—Journal of Biogeography 6:183–200.
- , and G. S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows.—Journal of Biogeography 4:135–142.
- , and R. J. Orth. 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—decapod Crustacea.—Estuaries 3:289–295.
- Holthuis, L. B. 1958. West Indian crabs of the genus *Calappa*, with a description of three new species.—Studies of the Fauna of Curacao and other Caribbean Islands 8:146–180.
- . 1949. The caridean Crustacea of the Canary Islands.—Zoologische Mededelingen 30:227–255.
- . 1959. The Crustacea Decapoda of Suriname (Dutch Guiana).—Zoologische Verhandlungen 44:1–296.
- Rhandler, N. A. 1964. Sponge as a shelter for young spiny lobsters.—Transactions of the American Fisheries Society 93:204.
- Ledoyer, M. 1959. Les Caridea de la frondaison des herbiers de phanérogames de la région de Tuléar.—Recueil des Travaux de la Station Marine d'Endoume (Supplement) 8:63–123.
- Lemaitre, R. 1981. Shallow-water crabs (Decapoda, Brachyura) collected in the southern Caribbean near Cartagena, Colombia.—Bulletin of Marine Science 31:234–266.
- , P. A. McLaughlin, and J. García-Gómez. 1982. The Provenzano group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic. Part IV. A review of the group, with notes on variations and abnormalities.—Bulletin of Marine Science 32:670–701.
- Lyons, W. G. 1970. Scyllarid lobsters (Crustacea, Decapoda).—Memoirs of the Hourglass Cruises, Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida 1(4):74 pp.
- McLaughlin, P. A. 1975. On the identify of *Pagurus brevidactylus* (Stimpson) (Decapoda: Paguridae), with the description of a new species of *Pagurus* from the western Atlantic.—Bulletin of Marine Science 25:359–376.
- , and A. J. Provenzano, Jr. 1974. Hermit crabs of the genus *Paguristes* (Crustacea: Decapoda: Diogenidae) from the western Atlantic. Part. II. Descriptions of six new species.—Bulletin of Marine Science 25:359–376.
- Manning, R. B. 1961. A redescription of the Palaemonid shrimp, *Leander paulensis* Ortmann, based on material from Florida.—Bulletin of Marine Science 11:525–536.
- . 1969. Stomatopod Crustacea of the western Atlantic.—Studies in Tropical Oceanography 8:1–380.
- , and F. A. Chace, Jr. 1971. Shrimps of the family Processidae (Crustacea, Decapoda, Caridea) from the northwestern Atlantic.—Smithsonian Contributions to Zoology 89, 41 pp.
- , and L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda).—Smithsonian Contributions to Zoology 306, 379 pp.
- Markham, J. C., and J. J. McDermott. 1981. A tabulation of the Crustacea decapoda of Bermuda.—Proceedings of the Biological Society of Washington 93:1266–1276.
- Miles, R. M. 1951. An analysis of "trashfish" of shrimp trawlers operating in Apalachicola Bay and adjacent Gulf of Mexico.—M.S. thesis, Florida State University, Tallahassee, 45 pp.
- Oliveira, L. P. H. de. 1940. Observações preliminares sobre a biologia dos Crustaceos do genero *Panopeus* Milne Edwards, 1834.—Memorias do Instituto Oswaldo Cruz, Rio de Janeiro 35: 153–171.
- Park, J. R. 1969. A preliminary study of portunid crabs in Biscayne Bay.—Quarterly Journal of the Florida Academy of Science 32:12–20.
- Pearse, A. S., J. J. Humm, and G. W. Wharton. 1942. Ecology of sand beaches at Beaufort, NC.—Ecological Monographs 12:135–190.

- Perez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*.—Fishery Bulletin 67:461–591.
- . 1971. Western Atlantic shrimps of the genus *Metapenaeopsis*, with descriptions of three new species (Crustacea: Decapoda: Penaeidae).—Smithsonian Contributions to Zoology 79, 37 pp.
- Powers, L. W. 1977. A catalogue and bibliography to the crabs of the Gulf of Mexico.—University of Texas Marine Science Institute, Contribution to Marine Science Supplement No. 20, 190 pp.
- Provenzano, A. J., Jr. 1959. The shallow-water hermit crabs of Florida.—Bulletin of Marine Science 9:349–420.
- Rathbun, M. J. 1918. The grapsoid crabs of America.—Bulletin of the U.S. National Museum 97: 1–461.
- . 1925. The spider crabs of America.—Bulletin of the U.S. National Museum 152:1–613.
- . 1930. The candroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae.—Bulletin of the U.S. National Museum 152:1–609.
- . 1937. The oxystomatous and allied crabs of America.—Bulletin of the U.S. National Museum 166:1–278.
- Rouse, W. L. 1970. Littoral Crustacea from southwest Florida.—Quarterly Journal of the Florida Academy of Science 32:127–152.
- Schnever, G. 1978. *In situ* observations on the behaviour of and biology of the tropical spider crab *Stenorhynchus seticornis* Herbst (Crustacea, Decapoda, Brachyura).—In: D. S. McLusky and A. J. Berry (eds.), Physiology and behaviour of marine organisms, pp. 297–302, Pergamon Press, New York.
- Shoup, J. B. 1968. Shell opening by crabs of the genus *Calappa*.—Science 160:887–888.
- Vermeij, G. J. 1982. Gastropod shell form, breakage and repair in relation to predation by the crab *Calappa*.—Malacologia 23:1–12.
- Voss, G. L. 1956. Protective coloration and habitat of the shrimp *Tozeuma carolinensis* Kingsley, (Caridea: Hippolytidae).—Bulletin of Marine Science 6:359–363.
- Wass, M. L. 1955. The decapod crustaceans of Alligator Harbor and adjacent inshore water of northwestern Florida.—Quarterly Journal of the Florida Academy of Science 18:129–176.
- Weinstein, M. P., and K. L. Heck, Jr. 1979. Ichthyofauna of seagrass Meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology.—Marine Biology 50:97–107.
- Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin 65:1–298.
- . 1974a. Marine flora and fauna of the northeastern United States: Crustacea: Decapoda.—NOAA Technical Report NMFS Circ-389, 50 pp.
- . 1974b. The swimming crabs of the genus *Callinectes* (Decapoda: Portunidae).—Fishery Bulletin 72:685–798.
- Yang, W. T. 1967. A study of zoeal, megalopal and early crab stages of some oxyrhynchous crabs (Crustacea: Decapoda).—Ph.D. diss., Univ. of Miami, Florida. 459 pp.

(LDC) Department of Zoology, University of Maryland, College Park, Maryland 20742; (KLH) Division of Environmental Research, The Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, Pennsylvania 19103.